Observations on the Social Behavior of the Southern Cricket Frog, *Acris gryllus* (Anura: Hylidae)

DON C. FORESTER
Department of Biological Sciences/Institute of Animal Behavior, Towson State University, Towson, Maryland 21204

AND

RICHARD DANIEL
Division of Biological Sciences, University of Missouri, Columbia, Missouri 65201

ABSTRACT.— Southern Cricket Frogs are prolonged breeders. During the reproductive season, males occupy calling territories from which they advertise for females. Mean territory size was 0.56 m^2 (0.03-1.36 m^2), and mean nightly movement by territorial males was 52 cm (0-205 cm). Territory size was not correlated with the number of days spent calling or with mating success. Observations on courtship behavior are presented.

Anuran species are categorized as either explosive or prolonged breeders (Wells 1977a). For species composing the former group, males and females arrive synchronously at the reproductive site. In many such species, males actively search out females, and mate discrimination by the female may be limited by male assertiveness. Explosive breeders are stimulated by heavy rainfall and breed for only a fews days afterwards. Prolonged breeders often partition the reproductive site into defended calling stations. Males advertise their position by persistent vocalization, and the arrival of receptive females is typically asynchronous. In species of this type, breeding is less dependent on seasonal precipitation, and reproductive activity may continue for months.

Studies on the reproductive behavior of anuran amphibians (particularly prolonged breeding species) have greatly increased during the past 15 years (for a review see Wells 1977a,b; Arak 1983). The purpose of this investigation is to quantify the breeding and courtship behavior of the Southern Cricket Frog, *Acris gryllus*, a small, terrestrial hylid indigenous to the southeastern United States (Neill 1950). During early spring and summer, males aggregate around pools and call. Chorusing may persist throughout the summer and calling males have been reported as late as early October (Wright and Wright 1949). Females appear to arrive at breeding pools asynchronously throughout the spring and

summer, with peak oviposition from late April through June (Mecham 1964), but egg clutches have been reported during early fall (Wright and Wright 1949).

Despite the fact that this species is among the most common anurans within its geographic range, little is known about its reproductive biology and social structure. Our attention shall focus on social interactions between males by testing the following hypotheses: (1) calling males occupy a territory, (2) there is a correlation between the size of a calling territory and the number of nights a male is observed at the pond, and (3) there is a correlation between territory size and mating success.

STUDY SITE

This study was conducted during June and July of 1975. The study site was a complex of three small sand pits situated in a mixed pine/deciduous flatwoods in Bryan County, Georgia. In most years the pits collect rain, and during the spring and summer are active reproductive sites for numerous amphibian species, including: the Southern Toad, *Bufo terrestris*; the Oak Toad, *Bufo quercicus*; the Eastern Narrow-mouthed Toad, *Gastrophryne carolinensis*; the Squirrel Treefrog, *Hyla squirella*; the Pine Woods Treefrog, *Hyla femoralis*; the Barking Treefrog, *Hyla gratiosa*; the Southern Cricket Frog, *Acris gryllus*; the Little Grass Frog, *Limnaoedus ocularis*; the Southern Leopard Frog, *Rana sphenocephala*; the Crawfish Frog, *Rana areolata*; the Bullfrog, *Rana catesbeiana*; the Carpenter Frog, *Rana virgatipes*; the Mole Salamander, *Ambystoma talpoideum*; the Red-spotted Newt, *Notophthalmus viridescens*; and the Striped Newt, *Notophthalmus perstriatus*.

Our study was confined to a small (D = 3.5 m) pool with gently sloping banks and a firm bottom. The margin of the pond was covered with patches of low, dense grass. This vegetation was cover for 8 to 12 calling male *A. gryllus*, and sparse enough to permit observation of the males with minimal disturbance.

METHODS

Individual Recognition.— Male cricket frogs may be distinguished individually based on their dorsal pattern (Bayless 1969). All males observed during this study had their dorsal patterns diagramed for reference. Because the breeding congress was small and never included more than eight males on any given night, individuals were easily recognized.

Calling Stations.— Male *Acris* call from land (Wright and Wright 1949), and in the present study were always within 1 m of the shoreline.

Males were located by entering the pond at a given point each night and searching the periphery from the water. When a male was located (usually by phonotaxis), a small marker was inserted into the substrate beside him. The markers were constructed from wooden dowels (D = 3 mm, L = 120 mm) to which a piece of white, waterproof tape had been attached. The identification number of the male and the observation date were printed on the tape with India ink. Calling males apparently were not disturbed by these activities.

Site Fidelity by Calling Males.— Each time the position of a calling male was marked, we recorded its spatial relationship (directional angle and distance in cm) to the most recently placed marker and to the original observation point. These measurements enabled us to plot the territories of individual males on graph paper. A Leitz planimeter (Model 3651-30) was used to calculate the area within each territory. Area values were based on an average of five separate measurements.

Statistical Analysis.— Spearman's rank correlation procedure (Zar 1974) was used to test for correlations between territory size and the number of nights a male was observed at the pond, and between territory size and mating success. The Spearman's rank procedure is a nonparametric test developed to process data obtained from a bivariate population that violates normalcy.

Operational Sex Ratio.— We calculated the operational sex ratio (OSR) for the males and females observed during this study. The OSR is defined as the average ratio of fertilizable females to sexually active males at any given time (Emlen and Oring 1977). The OSR may or may not reflect the overall sex ratio of the species, particularly for prolonged breeders in which females arrive asynchronously at the reproductive site.

RESULTS AND DISCUSSION

Site Fidelity and Size of Territory.— Individual males moved an average of 52 cm (0 to 205 cm) between nights. Table 1 compares the mean nightly movement of each male. Nine of eleven males were observed on enough nights to facilitate calculation of their calling territories. Mean territory size was 0.562 m^2 (0.028-1.362 m^2). We believe that this restricted movement and site fidelity warrant acceptance of our first hypothesis, that calling *Acris gryllus* males are territorial. We must reject our second and third hypotheses. There was no significant correlation between the size of a territory and the number of nights a male was observed at the pond (two-tailed Spearman's Rho, $r = -5.521$, $P > 0.05$). Neither was there a correlation between territory size and mating success (two-tailed Spearman's Rho, $r = 0.187$, $P > 0.05$) (see Table 2).

In our study, individuals appeared evenly spaced around the margin of the pond. On only one occasion was a calling male seen invading the calling territory of a conspecific. This occurred on 16 June, when, after 1 night at the pond, Male 10 moved into the adjacent territory of Male 1. The resident male moved 1.3 m counterclockwise and continued to call for 3 nights before disappearing from the pond. The only other example of an extensive spatial shift occurred on 13 June, when Male 5 moved 2 m counterclockwise in response to rising water, which inundated his original calling site. This shift did not cause a change in the calling territory of the adjacent male (Male 4), and Male 5 remained at his site for an additional 13 days before leaving the pond on 26 June.

Although we did not quantify intermale distance, such data are available for the species. Turner (1960) performed nearest neighbor analysis on a Louisiana population in December and April, and reported mean isolation distances of 1.94 m and 1.71 m, respectively.

Behavioral Observations.— Five of the 11 males monitored during our study (observations were made on 18 nights during a 37-night period) were observed to amplex a female. Male 4 successfully amplexed two females over a 4-night span. Five of the six amplecting pairs were observed within a 5-night period during mid-June. It is probable that additional matings occurred but went undetected, for we were unable to visit the pond every night and frequently departed while some males were still advertising.

The operational sex ratio at our study pond was skewed in favor of the males (5.6:0.3). However, it is likely that we underestimated the number of females present at the pond, and as a consequence we consider our OSR value conservative.

On three occasions during the course of our study, we had the opportunity to observe male-female interactions leading to amplexus. A summary of each follows.

(1) 13 June 1975. Male 4 was calling from his territory. With the exception of his pulsating vocal sac, he was hidden from direct view by dense grass. As we watched, a large female hopped into the circle of light. She appeared to be searching for the source of the sound. Her behavior included short, circling hops coupled with periodic cocking of her head from side to side. As the male continued to call, the female became increasingly active, crawling on the grass tussock and actually passing directly over the male on several occasions. Although the female circled eight times, the diameter of the circles never exceeded 8 cm. This sequence occupied just under 5 minutes and terminated when the male quickly emerged and amplexed the female. She neither resisted the male nor initiated contact with him.

Table 1. Linear movement of *Acris gryllus* males between consecutive nightly observations.

Male No.	Number of nights observed	Mean (cm)	Range (cm)
1	7	81.00	0-160
2	8	8.00	0-29
3	9	54.80	0-168
4	5	38.20	0-50
5	6	72.33	30-164
6	2	10.00	10-10
7	4	119.50	70-205
8	-	-	-
9	6	47.00	16-105
10	2	14.50	14-15
11	3	29.33	12-46

Table 2. Territory size, duration of calling, and mating success in a small breeding congress of *Acris gryllus*. No. nights observed = number of nights on which a male's calling position was marked. Days in residence = the span over which the male was known to be at the pond.

Male No.	Territory size (m^2)	No. nights observed	Days in residence	No. matings observed
1	0.502	9	10+	0
2	0.127	12	13+	1
3	1.373	16	37+	0
4	0.180	7	8+	2
5	1.362	11	18+	0
6	-	3	3	0
7	0.673	6	8	1
8	0.288	12	33+	1
9	-	2	4	0
10	0.028	6	8	0
11	0.545	7	23+	1
	$\bar{x}$ = 0.562	$\bar{x}$ = 8.27	$\bar{x}$ = 14.06	

(2) 14 June 1975. Male 7 was calling in an open spot between several clumps of grass. He lowered the pulse rate of his call and became active shortly before a female became visible. As the female approached, the male began to hop in tight circles (D = 4 cm). While moving, he continued to call. After 2.5 minutes, the male ceased calling and became stationary. Immediately the female approached to within 1 cm of the male's left side, and he quickly turned and faced her, snout to snout. After a 15-second pause, the male moved behind and amplexed the female.

(3) 11 July 1975. Male 11 was calling while a female sat 3 cm away, facing the opposite direction. They remained motionless for approximately 5 minutes. Suddenly the female began what we describe as a "quiver-hop" behavior, which involved quick, nervous movement of the forelimbs and elevation of the body 1 to 2 mm in a vertical position. After the female had exhibited this behavior twice in rapid succession, the male turned, moved quickly behind the female, and initiated amplexus.

Calling male cricket frogs formed duets, trios, quartets, and occasionally quintets. The significance of this call synchrony to *Acris gryllus* was not tested, but similar behavior is reported to be important during mate selection by other hylids. In a study of the Pacific Treefrog, *Hyla regilla*, females preferred the designated bout leader during call discrimination trials involving a single male quarteting with itself (Whitney and Krebs 1975). The authors concluded that bout leadership must somehow imply greater fitness to a responding female. We doubt that bout leadership is indicative of male fitness in *A. gryllus*, for two reasons: (1) bout leadership often changed during the course of an evening, and (2) bout leadership frequently changed from one night to the next. We suggest, as an alternative hypothesis, that antiphonal calling may enhance the fitness of the participating males by reducing broadcast interference. This role has been documented for the Spring Peeper, *Hyla crucifer*, a prolonged breeder of similar size and habits (Forester and Harrison, unpubl. ms.).

Among hylids, satellite behavior and sexual parasitism by noncalling males has been well documented (Perrill et al. 1978, 1982). To employ this behavioral strategy a noncalling male positions himself near a calling male and attempts to intercept females responding to the caller. Often, calling males respond agonistically to satellites as well as to other conspecific males that violate their calling territory. During our study, in more than 70 hours of observation, we observed neither satellite behavior nor agonistic encounters between males. Our failure to document social interactions between males is more likely a reflection of

low male density at our study pond, since both behaviors have been observed in dense populations of the closely related congener, *Acris crepitans*, in Indiana (S. A. Perrill, pers. comm.).

ACKNOWLEDGMENTS.— S. Simon and C. Boake provided assistance and companionship in the field. This project was funded, in part, by NSF Grant BNS 73 00795 to H. C. Gerhardt.

LITERATURE CITED

Arak, Anthony. 1983. Male-male competition and mate choice in anuran amphibians. Pages 181-210 *in* P. Bateson (editor). Mate Choice. Cambridge Univ. Press, New York.

Bayless, Laurence E. 1969. Ecological divergence and distribution of sympatric *Acris* populations (Anura: Hylidae). Herpetologica 25(3):181-187.

Emlen, Stephen T., and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215-223.

Mecham, John S. 1964. Ecological and genetic relationships of the two cricket frogs, genus *Acris*, in Alabama. Herpetologica 20(1):84-91.

Neill, W. T. 1950. Taxonomy, nomenclature, and the distribution of southeastern cricket frogs, genus *Acris*. Am. Midl. Nat. 43(1):152-156.

Perrill, Stephen A., H. C. Gerhardt, and R. Daniel. 1978. Sexual parasitism in the green tree frog (*Hyla cinerea*). Science 200:1179-1180.

_____, _____, and _____.1982. Mating strategy shifts in male green treefrogs (*Hyla cinerea*): an experimental study. Anim. Behav. 31:43-48.

Turner, Frederick B. 1960. Size and dispersion of a Louisiana population of the cricket frog, *Acris gryllus*. Ecology 41(2):258-268.

Wells, Kentwood D. 1977a. The social behaviour of anuran amphibians. Anim. Behav. 25:666-693.

_____ . 1977b. The courtship of frogs. Pages 233-262 *in* D. H. Taylor and S. I. Guttman (editors). The Reproductive Biology of Amphibians. Plenum Press, New York.

Whitney, Carl L., and J. R. Krebs. 1975. Mate selection in Pacific tree frogs. Nature 255:325-326.

Wright, Albert H., and A. A. Wright. 1949. Handbook of Frogs and Toads. 3rd ed. Comstock Publ. Co., Inc., Ithaca.

Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, N.J.

Accepted 28 June 1985